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THE MONIST.

ON EGG-STRUCTURE AND THE HEREDITY OF INSTINCTS.

THE INSTINCTIVE ACTIONS of animals are hereditary and can only be transmitted through the sexual cells. The problem of heredity from the physiological standpoint is, in brief, as follows: How can an egg, a simple vesicle filled with a viscous liquid which contains some solid constituents, be the bearer of such complicated mechanisms as the hereditary instincts? Two views are possible *a priori:* either the simplicity and homogeneity of the egg is only an illusion, and in reality it contains an invisible mysterious structure, of a similar degree of complexity to the adult animal; or the complicated mechanism of the instincts is the result of very simple circumstances which do not require any complicated structure for their transmission through the egg. All other possible suppositions are only compromises between these two possibilities. We shall here briefly present an argument in favor of the latter solution, which, we hope, will do away with some of the mystic aspects of heredity, and render a number of very complicated, albeit ingenious, theories redundant.

I.

The first view, which has been of late very ably expounded to the readers of *The Monist*, is held, among others, by Nägeli and Weismann; not so much, however, for the sake of accounting for the heredity of instincts as for the explanation of the continuity of forms in general. As the mysterious egg-structure which this theory presupposes is admittedly invisible, it is impossible to prove directly its non-existence. To the second view we are necessarily led when we attempt to analyse the instincts into their elements, which will deprive them of much that seemed very mysterious before. A few salient examples will be sufficient to throw a new light on the subject.

1. The larvæ of a certain butterfly (*Porthesia chrysorrhea*) hatch in Germany in the fall and hibernate in large numbers in a web on trees and shrubs. The warm spring sun drives the larvæ out of their nest, and they creep upward on the branches of the tree until they reach the highest points, where they find in the young buds their first food. As soon as they have eaten, they creep down on the branches until they find new buds or leaves which in the meantime have appeared in abundance. It is apparent that the instinct of the caterpillars to creep upwards after they awake from their winter sleep saves their lives. If they were not guided by such an instinct, those that crept downwards would perish from lack of food. How can such an instinct be transmitted by a single cell?

Experiments which I made eight years ago prove that the young caterpillars of Porthesia, as long as they are starving, are oriented by the light, i. e., the light causes them to bring their plane of symmetry into the direction of the rays of light, and to turn their oral pole toward the source of light. This process is purely mechanical. The light produces in the skin of the animal a change (probably chemical), and this produces, through the central nervous system, changes in the tension of certain muscles. Suppose the light falls upon the right side of the animal. This would lead to an increase in the tension of the muscles which turn the head and body of the animal to the right. As soon as the head of the animal is turned towards the source of light and its median plane is in the direction of the rays, the symmetrical points of the surface are cut by the rays of light at the same angle, and the chemical effect of the light is the same in each pair of symmetrical points of the surface of the animal. Correspondingly, the symmetrical muscles of both sides of the body are under equal tension, and there is no reason why the animal should deviate more towards one side than towards the other from the direction of the rays of light. Thus the animal goes towards the source of light. I may mention here, by the way, that this is also the mechanism by which the moth is forced into the flame. There is no such thing as an attraction of the moth by the light, but its fatal flight is only due to an orientation. We call those animals that are forced to turn their heads towards the source of light, and that consequently go towards the source of light, positively heliotropic.

Positive heliotropism of the young caterpillars of Porthesia leads them to the tips of the branches where they find their food. During the cold of winter they are rigid and immovable, the higher temperature of spring produces chemical changes in their bodies which causes them to move. The direction of motion, however, is dictated by the light. In the open air, where the light of the sky falls from all sides upon the animals, we may decompose each ray of light into a horizontal and vertical component. The horizontal components annihilate each other, and only the effect of the vertical component will remain. The animal, therefore, on account of its positive heliotropism, must creep upwards until it reaches the tip of a branch. Here it is held by the light. The chemical stimuli which are given to the animal by the young buds, determine, in a machine-like way, the feeding motions.

From these data we are able to answer the question, how much of a structure must be contained in the egg of Porthesia, in order to render possible the heredity of this curious instinct of the young caterpillars? The answer is, the egg must contain, first, a substance which is sensitive to light. This is possible without any complicated structure, even if we assume that the egg is only a mixture of different unformed substances. But this is only one of the elements which determine the positive heliotropism. The second circumstance is, as we have seen, the bilateral symmetry of the animal. For the transmission of the instinct, this, too, must be determined by the egg. This makes it necessary that a difference of the ventral and dorsal, of the oral and aboral pole is already intimated in the ovum, or originates early during the development. An unequal distribution of the substances of the egg would suffice to bring about this peculiarity.

But we have seen that the same larvæ, as soon as they have eaten, leave the tips of the branches and creep downwards. Why does the light not hold them permanently at the highest point of the branches? My experiments showed that the caterpillars of the animals are heliotropic only as long as they are starving, while they lose their heliotropism as soon as they are fed. This is not the only observation of this kind, for I have found a series of facts which show that chemical changes influence the irritability of the animal towards the light. We may imagine that the taking up of food either leads to the destruction of the substances which are sensitive to light, or leads to changes which inhibit their action. Thus the analysis of the curious instincts of the caterpillars of Porthesia does away with all complications, which might very easily lead to the assumption of mysterious structures in the egg.

2. While in this case, the external circumstances lead the young offspring to the feeding places, there is a second class of instincts in which the female deposits its eggs at places where the hatching larvæ find their food. A simple example of this group of instincts is the deposition of the eggs of the common fly. They lay their eggs upon putrefying meat, or cheese, and these substances are the material upon which the young larvæ of the fly feed. I have often made the experiment of putting pieces of fat and of meat from the same animal side by side in front of the window, but the female fly never made a mistake; the eggs were always deposited upon the meat and never upon the fat. Moreover, I tried to raise the young larvæ upon fat. As was to be expected with this kind of food they did not grow and soon died. It was possible to find out in these young larvæ the mechanics of this peculiar instinct of their mothers. The larvæ are oriented by certain chemical substances which emanate from a centre, and this orientation takes place in the same way as the orientation of the larvæ of Porthesia by the light. The rôle which the ray of light plays in the heliotropic experiments is played in these experiments by the lines along which

the molecules are carried away from the centre of diffusion into the surrounding medium. The chemical effects of these molecules upon certain elements of the skin influence the tension of the muscles in somewhat the same way as the rays of light do in heliotropic animals. We call the orientation of an organism through diffusing molecules, chemotropism, and speak of positive chemotropism if the animal is forced to bring its axis of symmetry into the direction of the lines of diffusion, and to turn its head towards the centre of diffusion. In this orientation again, each pair of symmetrical points of the surface of the animal is cut at the same angle by the lines of diffusion. It can easily be shown that the larvæ of the fly are positively chemotropic towards certain volatile substances, which are formed in putrefying meat and cheese, but which are not contained in fat. The substances in question therefore are volatile nitrogenous compounds. The young larvæ of the fly is guided by these substances to the centre of diffusion in the same way that the moth is guided into the flame. The female fly possesses the same positive chemotropism for these substances as the larvæ, and is therefore led to the meat. On the meat chemical stimuli seem to produce in the form of a reflex the deposition of the eggs. Neither experience nor conscious choice plays any rôle in these processes.

If we raise the question, what must be contained in the egg in order to transmit this instinct, we see that again two things are necessary. First, the presence of a substance, which either is influenced directly by the above-mentioned volatile compounds contained in putrid meat, or from which such changeable substances can originate. Secondly, conditions which lead to a bilateral symmetry of the embryo. But neither of these two conditions presupposes any mysterious structure in the egg, such as Nägeli, Weismann and others assume.

3. A third group of instincts is represented by the periodic migrations of animals. I select as an example the periodic depth migrations of sea animals. I should have preferred the more popular instance of bird migrations, if it were not for the fact that we can experimentally analyse the migrations of sea animals, whereas the migrations of birds have not yet been, and cannot very well be,

submitted to experimental research. A number of sea animals begin to migrate upwards towards the surface of the ocean in the evening, while in the morning they begin to migrate downwards. But the remarkable circumstance is, that these forms never go deeper than four hundred metres. The latter circumstance points out the light as the moving force in these depth migrations. Water absorbs light and the thicker the layer of water the more light is absorbed. It has been found that at the depth of four hundred metres a photographic plate is no longer affected. The animals which live free at the surface of the ocean, as far as I have been able to examine them, are all positively heliotropic. Those among them which undergo daily the above mentioned periodic migration into the depth, possess some peculiarities which can only be understood if we go a little deeper into the theory of animal heliotropism.

In addition to animals that are positively heliotropic, there are others that are negatively heliotropic: they bring their median plane also into the direction of the rays of light, but turn their *aboral* poles to the source of light. The difference between negatively and positively heliotropic animals is determined by the following circumstance: If the light falls upon one side of a positively heliotropic animal, an *increase* takes place in the tension of those muscles which turn the head of the animal towards the source of light, while in negatively heliotropic animals under the influence of one-sided illumination a *decrease* of the tension of the same muscles takes place. The consequence is that these negatively heliotropic animals are forced to move in a straight line away from the source of light, while the positively heliotropic animals are forced to move towards the source of light. Groom and I have examined the heliotropism of the larva of a Crustacean *Balanus perforatus* of which it was known that it undergoes such a periodic depth migration. One of the results of our experiments was that these larvæ are sometimes negatively and sometimes positively heliotropic and we succeeded in making them positively or negatively heliotropic at desire. In weak light, especially in gas light which contains relatively few blue rays, they became and remained positively heliotropic; while, in strong light, they invariably became very soon negatively heliotropic. This determines the depth migrations of these animals. If in the morning they are near the surface of the ocean, the strong light makes them negatively heliotropic, and forces them vertically downwards, as only the vertical component of the reflected light of the sky can orient these animals in the open sea. But as soon as they approach a depth of four hundred metres the light becomes so weak, that they now become positively heliotropic. They, therefore, must begin to migrate upwards again, but they cannot penetrate to the surface, as during the daytime they very soon reach a region of strong light, where they become negatively heliotropic. Thus they are kept suspended during the day time at a certain depth, which, however, is less than four hundred metres. But as soon as it grows darker and the intensity of the light in the water begins to decrease more and more, they must on account of their positive heliotropism, ascend into constantly higher regions; until during the night, when the intensity of the light is weak, they are held at the surface of the sea. In the morning they again become negatively heliotropic, starting their downward career over again.

But there is also another depth migration of a larger period, which corresponds more to the migration of the birds. In the Bay of Naples, as Chun has found, certain animals remain during summer, even during the night, at a greater depth without ever coming to the surface. This is probably caused by the higher temperature which makes certain animals, even in weak light, negatively heliotropic, while the same animals, at a lower temperature, remain positively heliotropic, even in the strongest light. I found these reactions among others in larvæ of *Polygordius*.

We therefore see that the instinct of migration, as far as it appears in the periodic depth-migrations of marine animals, can be explained by the presence of a substance which is sensitive toward light but which undergoes certain modifications with the change of light or temperature; and we can easily understand that a simple cell like the egg can be the carrier of this substance or some other substance from which it originates.

4. A number of animals show habits which we might, perhaps,

call protective instincts. Such animals hide in crevices or burrow. Thus they escape their enemies. For the heredity of this instinct equally simple circumstances suffice as for the heredity of the instincts characterised above. I have found that animals which force themselves into crevices do not do this in order to escape their enemies, but that these animals are forced to bring their bodies in contact with solid bodies. This kind of irritability is found in *Forficula,* in certain kinds of butterflies (*Amphipyra*), in larvæ of many insects and in worms. If one puts two plates of glass one above the other and so near that they are only separated by a small space, the above-mentioned animals force themselves between the two plates. They even do that when the plates are exposed to the full sunlight, in which case they are, of course, not protected from their enemies. They do it, moreover, when one-half of the box in which they are is quite dark, but does not offer them any such contact-stimuli as the two plates of glass.

This apparent protective instinct is a tropism of a similar kind as heliotropism, with this difference only that contact instead of light forms the cause of orientation. I called this class of phenomena orientation stereotropism, and could show that there is positive and negative stereotropism. In a hydroid, Tubularia, the polyp is negatively stereotropic, that is to say, it bends away from a solid body with which it comes in contact, while the root is positively stereotropic.

This peculiar form of irritability appears to play a rôle in a process which is frequently quoted, viz., the founding of a new nest by ants. At the time of sexual maturity, the males and females of ants become very energetically positively heliotropic, and this heliotropism may possibly direct them in their wedding flight. They leave their nests and follow the direction of the rays of light in a swarm. Procreation takes place in the air. As soon as it becomes darker, stereotropism overcomes the influence of light, the animals fall down and creep into crevices where they are held by their positive stereotropism and where they now deposit their eggs.

How contact-stimuli can affect life-phenomena is less easily explained than in the case of light. Possibly the pressure or friction against solid bodies influences the chemical processes in the cells. It is possible, too, that capillary effects may play a rôle. In any case, purely metabolic conditions are sufficient to explain these instincts and to do away with mystical ideas concerning their transmission through the egg.

II.

Through the above-mentioned facts we have been led to the view that, as far as the instincts are concerned, there is no reason to suppose that the egg contains other mysterious complicated structures than such as might possibly be expressed in the formulæ of the chemist. As soon as we decompose the complicated instincts into their elements, we understand that a simple cell like the egg can be the bearer of complicated instincts. The conditions in the egg which are required for this purpose are, to emphasise it once more, (1) polar differences in the chemical constitution in the egg substance, and (2) the presence of such substances in the egg as determine heliotropic, chemotropic, stereotropic, and similar phenomena of irritability.

But the egg is the bearer of another series of hereditary qualities, viz., of the animal's bodily system. Again we must raise the question how such a simple thing as the egg can be the carrier of circumstances which determine so complicated structures as are those of most animals. Again we have, *a priori*, the choice between two answers. Either the simplicity of the egg-structure is only an illusion, and we have in reality an invisible structure of the same degree of complexity in the egg as that of the adult organism; or, secondly, we do not require the mysterious structures for the transmission of such complicated mechanisms as seem to be necessary for the formation of organs, and comparatively simple conditions of the cellular substance in connexion with external circumstances are sufficient to explain the mystery.

It is well known that the egg of a sea-urchin is at first a single spherical cell which after fertilisation breaks up into many correspondingly smaller cells, from which aggregation of small cells a hollow sphere originates filled with liquid, the so-called blastula.

The wall of this hollow sphere is formed by the small cells of the egg. At this stage of development the larvæ are already able to swim around. A little later an increased growth takes place at one place of this hollow sphere, and the consequence is that this rapidly growing part is pushed into the interior of the hollow sphere. Thus the next embryonic phase is reached, the so-called gastrula stage. Finally in certain places of the gastrula, crystals of calcium salts are formed, and the skeleton originates, with the formation of which the embryo enters the so-called pluteus stage.

What must be contained in the egg in order to cause this succession of larval stages which finally lead to the adult form of the sea urchin? If we analyse the conditions which lead to the origin of these successive stages, we see that circumstances of no less simplicity are sufficient as for the heredity of instincts. The blastula is determined through two circumstances: (1) through the fact that the spherical egg is surrounded by sea water, and (2) that the osmotic and metabolic qualities of the protoplasm of the egg are of such a nature that liquid is pressed from the water into the interior of the sphere. In addition, capillary forces between the cells probably play a rôle, too, in the arrangement of the wall of the blastula. Thus the cavity of the blastula is formed. Therefore the egg does not need any other qualities for the heredity of the blastula stage, than certain chemical substances and the osmotic properties which are peculiar to almost all living protoplasms, and which we can imitate in the laboratory in artificial membranes.

The formation of the gastrula from the blastula presupposes that two different substances are present in the egg, which form the ectoderm and the entoderm. These may be separated from the beginning, and this would harmonise with the assumption which we have made in regard to the instincts, viz., that the different poles of the animal are already intimated in the unicellular egg by a corresponding distribution of the different substances. But it is not even absolutely necessary that this separation exists already in the original egg-cell. It is quite possible that migrations of substances take place in the blastula through osmosis, which lead to a gathering of specific entodermal substances at a certain place in the blastula. Here the entoderm is formed and invagination into the cavity of the blastula takes place.

The formation of a skeleton is nothing but the precipitation of crystals of certain salts of calcium. The conditions for this are purely physical, and without doubt are determined through metabolism and osmotic processes. Through their action such an increase in the concentration of the intracellular or pericellular liquids is produced in certain places that these crystals must be formed. Thus again, as in the case of instinct, the analysis of the phenomena renders the assumption of mysteriously complicated structures in the egg unnecessary.

That this idea is correct can be proven by the following experiment: If one brings newly fertilised eggs of a Sea Urchin (*Arbacia*) into sea water which has been diluted by the addition of one hundred per cent. fresh water, the contents of the egg take up so much water that the membrane of the egg bursts. Part of the protoplasm flows out from the egg without becoming entirely separated from the protoplasm which remains in the egg. Both droplets of protoplasm outside as well as inside the egg assume a spherical shape. Thus the egg which normally has the shape of a sphere assumes the shape of a dumb-bell. If these dumb-bell shaped eggs are brought back into normal sea water they develop. Very often, in fact in most cases, each of the two spheres of the dumb-bell will form a special blastula, so that such an egg gives rise to twins. The rest of the eggs form a single blastula which in the beginning is dumb-bell shaped but which later on becomes spherical. The later development of the twins as well as of the single Blastula is in general a normal one. This result of the experiments corresponds with our proposition that the blastula is determined by the osmotic entering of liquids into the interior of the segmented egg. If the egg is dumb-bell shaped a secretion must take place into the centre of both spheres of the dumb-bell. If, in this case, the substance which connects the two spheres is not torn we get two blastulæ and consequently twins. But if the hydrostatic pressure inside of the spheres or any other conditions bring about a communication between the liquid contents of the two hollow spheres, then only one blastula and only one embryo is formed. If the egg contained a mysterious structure which pre-determines the future embryo, we should expect that *one distorted* larva would originate from the egg transformed into a double sphere, and not two or one perfect larvæ, as is generally the case.

Still another field of phenomena makes it impossible to attempt to lead back the hereditary forms to mysterious egg-structures of a highly complicated nature. I mean the phenomena of heteromorphosis. By heteromorphosis we mean the substitution of an organ by another one which is different morphologically and physiologically. Tubularia, a hydroid, consists of a stem which carries on one end, a polyp or head and on the other end a root or foot. If one cuts off the foot and surrounds the wound with sea water from all sides, a new head is formed instead of a foot. We thus have an animal which has a head on each end of its body. But if we bring the wound in contact with a solid body, such as the bottom of the aquarium, a foot is formed. If we cut a piece out of the stem, which is only of the size of a polyp and surround it by water from all sides, a head is formed at either end, but as there is no material left between the two heads, we thus obtain Janus heads, without stem and foot.

These two kinds of experiments may suffice to intimate that as soon as we begin to analyse the process of morphogenesis, we find it unnecessary and even faulty to assume a complicated structure in the egg in order to explain the continuity of forms.

Finally, I should like to emphasise one circumstance which repeats itself in the history of science and especially biology. Whenever we are not able to explain complicated phenomena, we are at first inclined to imagine that their cause must be of similar complication to the phenomenon itself. Thus the idea of an invisible complicated egg-structure was adopted in order to explain the heredity of instincts and forms, and thus the ideas of mysterious structures of the ganglionic cells are still held by many in order to explain the mechanism of reflex phenomena and instinct. All these attempts fail for the reason that they try to explain complicated phenomena without having them analysed into their simpler constituents. As long as we consider instincts as units which cannot be decomposed, we must naturally imagine the heredity of these instincts under the mental picture of a mysterious clock-work contained in the egg. But as soon as we analyse them, we are confronted with very simple phenomena which make the idea of a mysterious invisible structure as the cause of these instincts unnecessary.

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